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SCOULERIA SISKIYOUENSIS (SCOULERIACEAE), A NEW RHEOPHYTIC MOSS ENDEMIC TO SOUTHERN OREGON, USA

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Abstract

Scouleria siskiyouensis Shevock & D. H. Norris, a new species restricted to rivers and streams in southwestern Oregon is described and illustrated. This species appears related to the widespread *S. aquatica* Hook. *in* Drummond of western North America but is distinguished by a combination of features including lamina bistratose except for a few cells at immediate leaf margin unistratose, leaves lanceolate to ovate-lanceolate and with leaf apex acute to acuminate.

Key Words: Aquatic mosses, rheophytes, *Scouleria aquatica*, *Scouleria marginata*.

Scouleria Hook. is a very distinctive genus of rheophytic mosses. Described by Hooker in 1829, the dark coloration and growth habit resemblance to certain rheophytic *Racomitrium* Brid. s.l. (*Codriophorus* P. Beauv. and *Bucklandiella* Roiv.) and *Schistidium* Bruch & Schimp. species probably contributed to its initial placement by early bryologists in the Grimmiaceae. The presence of systylious capsules is also similar to species of *Schistidium*. *Scouleria* is immediately recognized in the field by its habitat (aquatic in rapidly flowing streams and rivers); by its size and coloration (drying nearly black with leaves mostly about five mm or more broad); and by its capsule morphology (nearly sessile, large and globose with very thick capsule walls and presence of a columella).

As a rheophytic genus, *Scouleria* has one of the most unusual distributions of bryophytes: western North America, North Asia (Siberia and the Russian Far East), and southern South America (Churchill 2007). In North America, *Scouleria* primarily occurs along the Pacific Slope from Alaska to California with scattered disjunct populations inward to Montana but is not found in the eastern half of the continent. Only two species of *Scouleria* have been recognized for North America. These two species are readily recognized in the field by a hand-lens examination of the leaf border. In *Scouleria aquatica* the border is merely thickened but flat caused by either enlarged cells or by the development of a bistratose layer at the margin. However, in *Scouleria marginata* E. Britton, the margin appears inflated and rounded due to thickened multistratose cells along the margin forming a more prominent border, especially seen on older leaves. These two species rarely grow sympatrically. *Scouleria marginata* prefers larger river systems and generally lower elevations whereas *S. aquatica* has a much broader range of ecological attributes occurring from near sea level to the headwaters of tributary streams.

For over 150 yr *Scouleria* remained in the Grimmiaceae but the largely morphological work conducted by Churchill (1985) convincingly elevated *Scouleria* to family status. Recent molecular evidence also supports the recognition of this family of rheophytic mosses (Tsubota et al. 2003; Carter et al. 2014).The other genus attributed to this family, *Tridontium* Hook. f., is monospecific, and is endemic to Australia and New Zealand. *Scouleria* is a genus that is easily recognized in the field. It is restricted to rapidly flowing unpolluted rivers and streams where plants are seasonally submerged then exposed on boulders and rock walls as rivers decrease in flow. When hydrated, *Scouleria* is dark green in color but upon drying becomes nearly black. *Scouleria* generally occurs in large patches and when in a dry state these blackened *Scouleria* populations can be recognized on large boulders and rock walls from a distance of several meters. On a worldwide basis all members of *Scouleria* seem to be the ultimate rheophyte, annually receiving severe scouring during peak flows when sediment yields are increased, deep submersion, an extended period in white water rapids, followed by a period of desiccation during which they are generally exposed in full sun during the hottest months of the year.

All species of *Scouleria* have a prominent morphologic feature that exhibits an unusual structure for a moss leaf. In addition to the usual feature of alar cells and median laminal cells (isodiametric and thick-walled in *Scouleria*) there is an area of several rows of elongate and glistening white-walled cells which is seen as an intramarginal limbidium. This intramarginal limbidium seems to be unique to the genus but its prominence varies greatly from leaf to leaf even on a single stem. Some leaves may have only a few cells between the alar and median cells while other leaves may have an intramarginal limbidium that comprises most of the area of the leaf. The variability in the prominence of the intramarginal limbidium does not seem to be related to species differences within the genus, and it seems also unrelated to apparent habitat differences. This limbidium although often is the dominant visual feature of some leaves apparently has no taxonomic importance beyond merely signaling the generic identification. An additional generic character for *Scouleria* is the frequency of rhizoids on the abaxial base of the costa.

While the genus is easy to determine, the recognition of species has been more difficult. The actual number of species based solely on morphological features has ranged from three to five species, and part of this recognition was based on geography rather than a good set of morphological characters. Like many rheophytes, the aquatic growth form creates a large array of morphological character variations generally useful for identification purposes such as leaf shape, leaf size and leaf border. Most keys developed to separate *Scouleria* species have relied on cross sections of leaves to describe the patterns and locations of various levels of bistratosity. Crosby et al. (2000) treat the genus as comprised of three species; two species in the Northern Hemisphere and one in the Southern Hemisphere. However, two additional species, *S. rschewinii* Lindb. & Arnell described in 1890 and *S. pulcherrima* Broth. described in 1916 from Siberia and the Russian Far East were subsequently reduced to synonymy within the geographically widespread *S. aquatica* (Churchill 1985). As late as 1970, sporophytes were unknown for these two Russian taxa (Savič-Ljubickaja and Smirnova 1970). However, Churchill (2007) acknowledges that much variation exists within the *S. aquatica* complex and other taxonomic arrangements at variety or species level may be warranted through future molecular study. While sporophytic characters can be highly informative between members within a genus, in *Scouleria* capsules are generally infrequently produced, are of short duration and look basically the same in shape and color. Even when capsules are present on herbarium specimens they are rather fragile and peristome teeth or their remnants are easily lost or detached. The only distinction in capsule morphology described in the genus to date is the lack of peristome teeth in *S. marginata*, a species endemic to the Pacific Slope of North America from British Columbia to California with isolated populations in Idaho and Montana (Lawton 1971; Christy et al. 1982; Churchill 1985, 2007; Norris and Shevock 2004a). Kurbatova (1998) states that the seta is longer in *S. aquatica* var. *pulcherrima*, but we have not seen Russian *Scouleria* with capsules for comparison to North American taxa.

Fieldwork contributing toward a bryoflora of California (Norris and Shevock 2004a) led to the collection of many bryophytes, especially from the northern extension of the California Floristic Province within southern Oregon. This area is well-known as one of the biodiversity hot spots for vascular plants and contains a high level of endemism (Norris 1997). The area of the Kalmiopsis Wilderness on the Siskiyou portion of the Rogue River-Siskiyou National Forest is exceptionally important as an evolutionary refugium. The same area is also rich in bryophyte diversity. Following examination of *Scouleria* collections from that general region it was determined that an undescribed species was likely at hand based on vegetative leaves that are strikingly more lanceolate and acute at apex. Under a compound microscope, a cross section displayed far greater development of bistratosity across the lamina than seen previously in the genus. However, describing a new *Scouleria* from North America was deemed to require a critical examination of *S. aquatica* throughout its range including plants from the Russian Federation. Due to the view of extreme plasticity displayed among morphological features of rheophytes in general and wide variation reported within the *S. aquatica* complex in particular, this issue was not pursed further at that time although this entity was referenced in the *Scouleria* key as 'species A' (Norris and Shevock 2004b). Eventually a molecular study was initiated to determine the affinities of *Scouleria* within its geographical range. That study (Carter et al. 2014) confirmed that the Russian species are worthy of species rank, *S. aquatica* is restricted to North America, and that the southwestern Oregon plants represent a species new to science and is described herein.

Taxonomic Treatment

Scouleria siskiyouensis Shevock & D. H. Norris, sp. nov. (Figs. 1–2). —TYPE: USA, Oregon, Douglas Co., Coos Bay District, Bureau of Land Management, Middle Fork Coquille River along highway 42 west of Roseberg at milepost 26, former site of Bear Creek Recreation Area, T30S, R9W, section 9, 42°58′9.2″N, 123°45′57.8″W, 850 ft, 19 Mar 2005, *Shevock and Kellman 26365* (holotype: CAS; isotypes: H, HYO, KRAM, MHA, MO, NY, OSC, UBC, VBGI, UC).

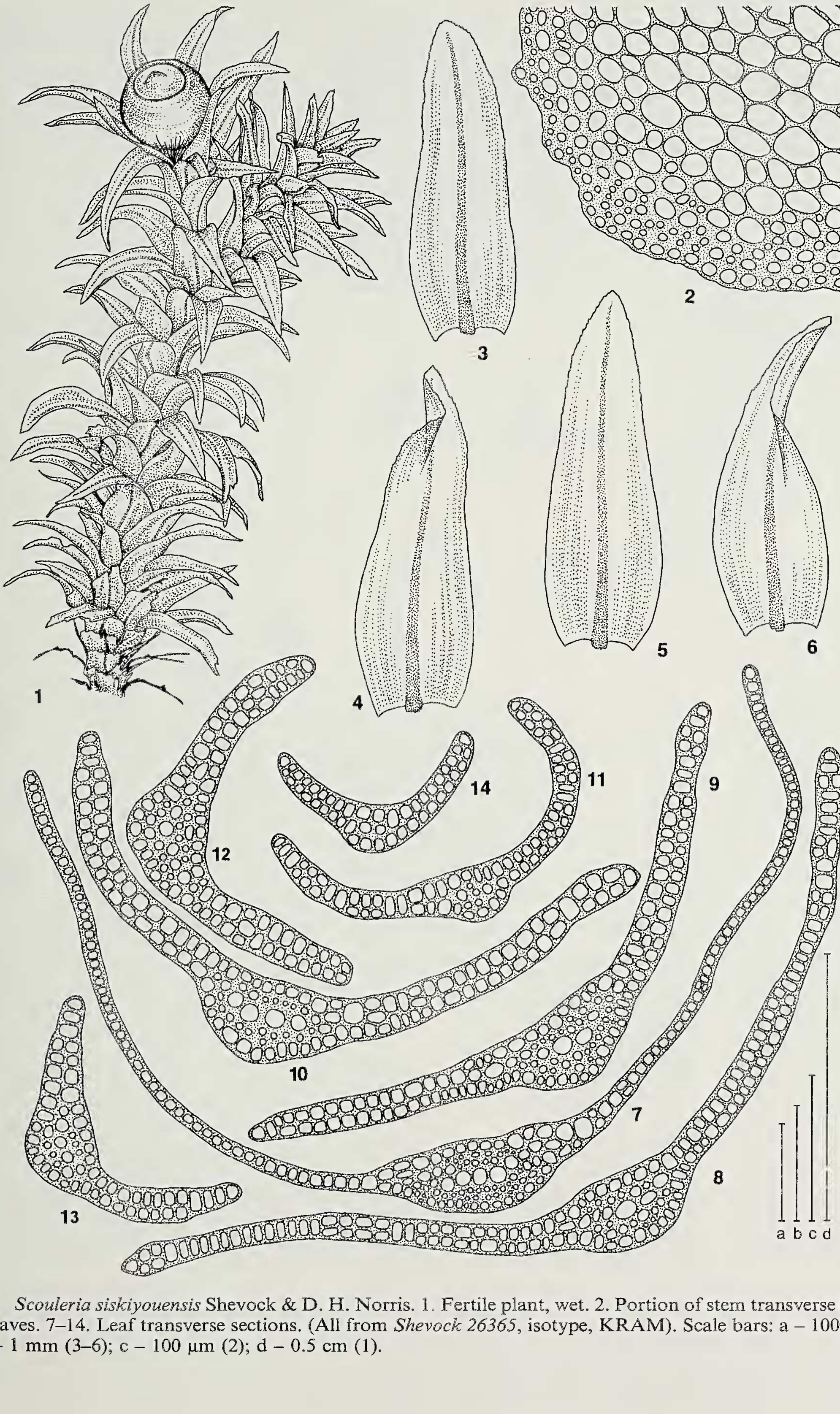

FIG. 1. *Scouleria siskiyouensis* Shevock & D. H. Norris. 1. Fertile plant, wet. 2. Portion of stem transverse section. 3–6. Leaves. 7–14. Leaf transverse sections. (All from *Shevock 26365*, isotype, KRAM). Scale bars: a – 100 µm (7–14); b – 1 mm (3–6); c – 100 µm (2); d – 0.5 cm (1).

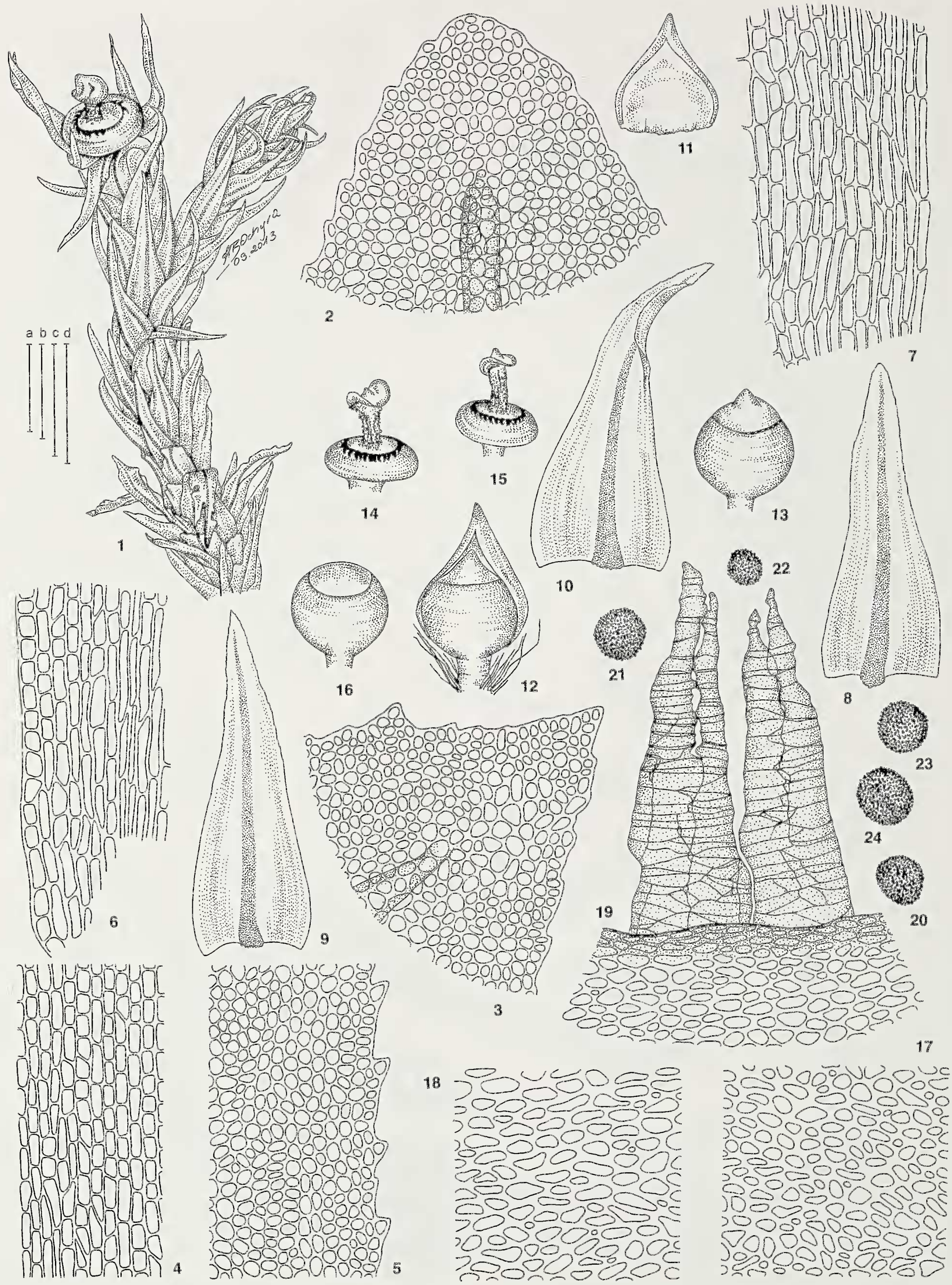

FIG. 2. *Scouleria siskiyouensis* Shevock & D. H. Norris. 1. Fertile plant, dry. 2–3. Leaf apices. 4. Mid-leaf cells. 5. Mid-leaf cells at margin. 6. Basal angular cells. 7. Basal juxtacostal cells. 8–10. Perichaetial leaves. 11. Calyptra. 12. Operculate capsule with calyptra, wet. 13. Operculate capsule, wet. 14–15. Young systylious capsules, dry. 16. Old capsules with destroyed peristome, dry. 17. Exothecial cells at base of urn. 18. Mid-urn exothecial cells. 19. Exothecial cells at orifice and portion of peristome. 20–24. Spores. (All from *Shevock 26365*, isotype, KRAM). Scale bars: a – 1 mm (1, 11–16); b – 1 mm (8–10); c – 100 μm (17–24); d – 100 μm (2–7).

Plants aquatic, usually in rapid water of streams and rivers, often rather closely branched, mostly to 8 cm long. Plants dark green to brownish-green in younger portions, glossy black in older portions, frequently with most of the leaf laminae removed by water scouring, leaving only the costa. Leaves to 5 mm long, 1.5–3.5: 1, not decurrent. Leaf apex acute to acuminate with apex not cucullate. Leaves broadly keeled above midleaf. Leaf margins serrulate to serrate to finely dentate, usually plane. Leaves mostly bistratose, but with margins unistratose for several cells along the border. Laminal cells of median limb isodiametric, about 10 µm or nearly so, smooth. Laminal cells of median portions of the sheathing base to 12 µm broad, short-rectangular, mostly 2–3: 1, thick-walled with lumen; wall ratio 1–2: 1, mostly not pitted. Costa on adaxial side having 6–8 cell rows of rectangular epidermal cells, filling more than 20% of leaf, tapering very little to the subpercurrent apex, with rhizoids cloaking its abaxial basal 1/5 or more. A broad and almost white to pale inframarginal limbidium usually present, often restricted to proximal one quarter of leaf, but sometimes extending to near leaf apex with this variability in extent shown even on leaves of the same clone. Axillary hairs 5–6 cells long to 100 µm with 2 short but concolorous basal cells, cylindric and of constant diameter thick-walled (lumen: wall ratio 1.5–3: 1). Rhizoids red-brown with somewhat warty surfaces, to 35 µm in diameter at insertion, mostly on oldest parts of stem, and also on the adaxial face of the costa, mostly below mid-leaf. Plants presumed dioicous, perigonia not seen; perichaetial leaves generally reduced in length and width compared to vegetative leaves. Seta mostly less than 1 mm long straight and smooth emerging from a short vaginulum with a heavy cover of paraphyses; calyptra covering half or less of maturing capsule, cucullate, smooth, naked. Capsule systylious, mostly 2.5–3 mm long, nearly globose when young and operculate but shrinking and becoming ring-like after dehiscence of apiculate operculum, then becoming 2–3 times broader than tall with the longitudinally ribbed columella occupying the central axis of the shortened capsule and with the spores surrounding that columella. Median exothecial cells to 15 µm wide, 1–2.5:1 rather thick-walled, arranged in regular longitudinal rows. Peristome of 32 fragile, short, triangular teeth, to 400 µm long, reddish when young, aging brown, inserted 1–2 cells below mouth of capsule, smooth with prominent dorsal trabeculae, blunt at apices, reflexed when dry, slightly incurved when wet. Teeth cover only a very small portion of the capsule mouth. Spores spherical, generally light brown, to 40 µm in diameter, ornamented with low anastamosing ridges.

Paratypes: USA, OREGON. **Coos Co.**: South Fork Coquille River along forest road 33 at Elk Creek Falls, Rogue River-Siskiyou National Forest, 165 ft, 21 Mar 2005, *Shevock 26421* (CAS, CONC, H, KRAM, LE, MO, NY, UBC, UC); Same location, 14 Jun 2005, *Wagner m1697* (CAS, OSC); Myrtlewood Grove Campground, 375 ft, 21 Mar 2005, *Shevock 26438* (CAS, MO, NY, UC). **Curry Co.**: Elk River Road about 17 mi E of highway 101, Rogue River-Siskiyou National Forest, 8 Mar 1972, *Norris 21977* (UC); Elk River Road about 17 mi E of highway 101, Rogue River-Siskiyou National Forest, 8 Mar 1972, *Norris 21979* (UC); about 10 mi SE of highway 101 east of Port Orford, 300 m, 25 Jan 1995, *Norris 84649* (CAS, H, LE, UC); Elk River Road 1.4 mi E of fish hatchery, 530 ft, 1 Mar 2013, *Shevock 41901* (CAS, CONN, DUKE, E, F, H, KRAM, LE, MHA, MO, NY, OSC, UBC, UC, US); Bear Creek at confluence with Elk River 2.2 mi E of fish hatchery, 550 ft, *Shevock 41906* (BOL, CAS, COLO, CONC, E, H, KUN, MO, NY, OSC, UC); Bear Creek at confluence with Elk River 10 mi E of fish hatchery, 850 ft, *Shevock 41910* (CAS, CONC, CONN, H, HO, KRAM, L, LE, MHA, MO, NY, OSC, TNS, UBC, UC, US); Redwood State Park about 8 mi E of Brookings, along Chetco River, 3–9 Sep 1950, *Koch 3245* (UC); Redwood State Park about 8 mi E of Brookings, along Chetco River, 3–9 Sep 1950, *Koch 3270* (UC); Redwood State Park about 8 mi E of Brookings, along Chetco River, 3–9 Sep 1950, *Koch 3290* (UC); Chetco River, Siskiyou National Forest, T39S, R12W, S13, 400 ft, 17 Oct 2002, *Jones 3954* (OSC); South Fork Chetco River just above confluence with Chetco River, at milepost 8, Rogue River-Siskiyou National Forest, 155 ft, 19 Jan 2013, *Shevock and Lambio 41752* (BOL, CAS, COLO, DUKE, E, F, H, HO, KRAM, L, LE, MHA, MO, NY, OSC, UBC, UC, US); Winchuck River at forest boundary, 0.5 mi west of Winchuck Campground, Rogue River-Siskiyou National Forest, 175 ft, 19 Jan 2013, *Shevock and Lambio 41759* (CAS, CONC, H, KRAM, LE, MHA, MO, NY, OSC, UBC, UC). **Josephine Co.**: South Fork Taylor Creek along forest road 25 near Tin Can Campground, Rogue River-Siskiyou National Forest, 1000 ft, 28 Feb 2013, *Shevock and Loring 41881* (CAS).

Taxonomic Relationships

Scouleria siskiyouensis has gone undetected due to its similarity to other *Scouleria* species in southern Oregon. The plants form robust colonies similar in appearance to populations of both *S. aquatica* and *S. marginata*. These taxa, however, are readily separated. When sporophytes are present, *S. siskiyouensis* has 32 fragile peristome teeth reflexed on the mouth of the capsule while peristome teeth are absent in *S. marginata*. Gametophytically the leaves in *S.*

siskiyouensis are primarily bistratose across the median region but cells adjacent to the border are unistratose. *Scouleria marginata* on the other hand is unistratose across the lamina (rarely with bistratose streaks) but the leaf margins are multistratose and appear considerably thickened called 'pseudocostae' by Churchill (1985). *Scouleria aquatica* resembles *S. siskiyouensis* but it is generally smaller in stature with a more rounded leaf apex. Sporophytes appear to be identical between these two species although they are exceedingly more common in *S. siskiyouensis* compared to *S. aquatica*. A leaf cross-section is the most reliable method of species recognition between these related taxa. *Scouleria aquatica* can be distinguished from *S. marginata* by the marginal cells of the vegetative leaves that are in only one layer or occasionally with bistratose streaks and are somewhat enlarged and thin-walled compared to the 4+ layers of stereid like cells in *S. marginata*. This feature of having multistratose borders can be observed with a hand-lens in *S. marginata*. *Scouleria aquatica* has peristome teeth, which differ from the eperistomate *S. marginata*. Based on a recent molecular study (Carter et al. 2014), *Scouleria siskiyouensis* is sister to *S. aquatica*.

Habitat and Ecology

Scouleria siskiyouensis is restricted to fast flowing, unpolluted rivers and streams with large boulders. Plants seem to require seasonal submergence, an extended period in the splash zone, then a period of complete desiccation. Several other rheophytic mosses can be associated with *Scouleria siskiyouensis*. *Scleropodium obtusifolium* (Mitt.) Kindb. and to a lesser degree *Codriophorus aciculare* (Hedw.) P. Beauv. and *Schistidium rivulare* (Brid.) Podp., are the most common associates. *Scouleria* is a genus that requires seasonal submersion, cold, clean water, and periods of desiccation during the dry summer months. Changes in such hydrologic function could rapidly cause the extirpation of this species from those locations. *Scouleria* can also be very localized even in river and stream systems where it occurs. Plants are found on large boulders or walls of bedrock micro-sites where they cannot be displaced during floods or periods of peak flows. Populations can occupy up to a meter wide band in the water column depending on river flow. Generally, *Scouleria* occurs just below the high water zone. A period of time in the splash zone among white-water rapids appears to be critical for the establishment of sporophytes. Being both dioicous and a rheophyte may account for limited success of sporophyte production. As an aquatic moss, fertilization has to occur while the plant is hydrated and free water is readily available and plants need to stay hydrated (in the splash zone) while sporophytes are maturing. However, among North American *Scouleria*, *S. siskiyouensis* produces sporophytes considerably more frequently with mature capsules appearing during the winter season and sporophytes also appear to develop in series as water levels fluctuate between winter storms. Sporophytes of *Scouleria siskiyouensis* have been observed in all of the populations documented to date. In *S. aquatica* and *S. marginata*, sporophytes are generally produced later in the year depending on elevation, however, based on our field observations both species produce sporophytes more frequently in Oregon than in adjacent California.

Among rheophytic mosses the peristome teeth in *Scouleria* are rather unusual. The role of the peristome is traditionally understood as a means of facilitating spore dissemination by opening of the capsule mouth at times when environmental conditions are favorable for spore release. Peristomate bryophytes differ in the patterns of reflexing and inflexing generally based upon ambient humidity. In *Scouleria*, the peristome seems to have neither function. Peristome teeth in *Scouleria* are so small and fragile that they are unlikely to carry their unusually large spores toward the capsule mouth to aid in dispersal. The mouth of the capsule is exceedingly broad in relation to the tiny ring of peristome teeth, and therefore, these teeth provide no means of restriction of the capsule mouth. The release of spores in *Scouleria* actually occurs when the systylious globose capsule shrinks longitudinally from the operculum and columella like a donut causing the bulk of the spores to be forced out by this compression action. The remaining spores lodged in the base of the capsule are disseminated as the capsule wall disintegrates. Additional spores can also are removed from the opened capsules in the event water levels rise again after capsule dehiscence. The peristome teeth in *Scouleria* are but mere ornamentations and seem to be a useless structure, normally reflexed along the capsule wall. Of the six species of *Scouleria* worldwide, peristome teeth have been lost in only *S. marginata*.

Distribution

Populations of *Scouleria siskiyouensis* are currently restricted to southwestern Oregon, primarily in the Siskiyou portion of the Rogue River-Siskiyou National Forest within the Coast Range Ecoregion. Population elevations range from 150 to 1000 feet. This species is a very narrow rheophytic endemic with the distance between the northern and southern occurrences being only 68 air miles. We anticipate additional populations of *S. siskiyouensis* within this range will be discovered as more bedrock river and stream habitats are surveyed along the western and northern boundaries of the Siskiyou portion of the Rogue River-Siskiyou National Forest and adjacent BLM Coos Bay District lands. Although the southernmost Oregon occurrence along the Winchuck River is just 1.75 air miles north of the California/Oregon border, we are of the opinion that locating a California occurrence may be limited. We were unable to locate *S. siskiyouensis* during field sampling in the adjacent Smith River watershed in California although both *S. aquatica* and *S. marginata* are present but as small, isolated populations. The riparian zone within the Smith is not optimum habitat for the new *Scouleria* taxon due to the dominance of serpentine geology resulting in less riparian vegetation along river and stream corridors.

Conservation Implications

The majority of the known occurrences of *Scouleria siskiyouensis* occur on public lands administered by either the USDA Forest Service or the USDI Bureau of Land Management, thereby offering greater opportunities for long-term conservation. In addition, many rivers and perennial streams have added layers of protection by law and regulation to conserve riparian values and anadromous fisheries, especially those occurrences along Congressionally designated Wild and Scenic Rivers. Dams, however, could be fatal to this species since river hydrology and ecology would be significantly altered.

Key to Oregon *Scouleria*

1. Plants with leaves lanceolate to ovate lanceolate, leaf apex acute to acuminate; transverse section of leaves primarily bistratose except for a few unistratose cells at immediate leaf margin . . . . *Scouleria siskiyouensis*

1′. Plants with leaves mainly ovate, leaf apex almost consistently obtuse to bluntly-rounded; transverse section of leaves unistratose or with occasional bistratose streaks or with thickenings (multistratose layers) along the immediate margin

   2. Leaf margins unistratose or occasionally with bistratose streaks or larger cells along margin but without areas of greater thickness; capsule with 32 reddish short peristome teeth. . . . . *Scouleria aquatica*

   2′. Leaf margins prominently thickened throughout, somewhat cartilaginous with 4–6 layers of cells in the immediate margin; capsule lacking peristome teeth . . . . *Scouleria marginata*

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